Characteristics of the Western Atlantic Reef-fish Fauna

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The western Atlantic reef-fish fauna is better known than that of any similar area of the world, with the possible exception of the Hawaiian Islands. This should give one an idea of how extremely limited is our knowledge of the faunistically richer and geographically more vast Indo-Pacific region. Most of our knowledge of western Atlantic reef fishes has accumulated during the past 15 years, and this can be attributed to three factors 1) the tremendous increase in numbers of ichthyologists investigating the fauna, 2) the development of SCUBA gear and rotenone-based fish toxicants, and 3) the exploratory fishing activities of the U. S. Bureau of Commercial Fisheries. Of the many new species that have been discovered during this time, a high percentage are small, cryptic reef dwellers, particularly of the families Clinidae and Gobiidae. For example, of the 46 clinids (including the Chaenopsidae and Tripterygiidae) and 41 gobies listed by Böhlke and Chaplin (1968) for the Bahamas, 18 species in each family have been described since 1953. In addition, two Bahamian gobies and one clinid have since been named, and at least a dozen other known Bahamian species have yet to be described. Many others undoubtedly remain to be discovered. The same relative totals for the gobies reported by Starck (1968) from Alligator Reef, Florida, are even more illuminating; 14 of the 27 species listed have been described within the same period. Knowledge of most groups of marine invertebrates is even substantially less than for the fishes.

Although it is unlikely that man's activities will result in the wholesale extermination of reef-fish species from extensive geographic areas, such as has occurred for certain freshwater forms, the need for accurate and relatively complete lists from the various parts of the western Atlantic is no less acute. The faunistic studies for Puerto Rico (Evermann and Marsh, 1902), Haiti (Beebe and Tee-Van, 1928), and the Dry Tortugas (Longley and Hildebrand, 1941) all are very valuable contributions; however, many of the small reef dwellers were not collected because of the primitive diving gear and lack of completely effective fish toxicants. Other use-

ful works are those by Cervigón (1966) for Venezuela and by Caldwell (1966) for Jamaica, although both of these suffer somewhat from the paucity of reef collections below the 50 foot level. The paper by Birdsong and Emery (1968), which lists collections made by Birdsong and Walter A. Starck II from the poorly known western Caribbean, is also a valuable contribution. Other important recent collections of fishes, for which published faunal reports have not yet appeared, are from Puerto Rico and the Virgin Islands (J. E. Randall), Grand Cayman Island (J. C. Tyler and C. R. Gilbert), Haiti (Tyler, T. Devany, and H. A. Feddern), Old Providence Island (Tyler and Gilbert), British Honduras (D. W. Greenfield), and from various islands in the Lesser Antilles (Tyler and W. N. Eschmeyer). The most complete faunal studies, however, are those by Böhlke and Chaplin (1968) for the Bahamas, and by Starck (1968) for Alligator Reef and vicinity, in the northern Florida Keys. The latter undoubtedly is the most thorough study of a limited reef area done anywhere in the world. These two works, together with the paper by C. R. Robins (in press), have provided much of the information upon which the present paper is based.

Despite the large amount of data that has recently accumulated, it is impossible to determine accurately the distribution patterns for many species of western Atlantic reef fishes. Although basically due to the incomplete geographical coverage of our collections, the difference in abundance of various species, either on a permanent basis or at a particular time, is an important contributing factor. This is especially true of the smaller forms. Lack of consistency in the composition of the coral reef-fish fauna from one time to another is, in fact, the rule rather than the exception. Thus, collections made over a limited period of time will almost invariably miss the bulk of the species. For example, Starck (1968) recorded a total of 517 species of fishes from Alligator Reef, Florida, of which 389 are true members of the reef community; however, the most thorough collections from this area at any one time (i.e., day) probably would not exceed 100 or 125 species. Sometimes rarity of usually common species is the result of introduction of occasional strays into an unfavorable ecological situation. Starck's (1968) list includes at least 12 species that evidently fall into this category, all of which are widespread in the Bahamas. Two of these (the chaetodontids *Centropyge argi* and *Prognathodes aculeatus*) main-

tain permanent populations just north of Miami, where the water is consistently more clear than in the Florida Keys, thus leading Starck to conclude that water turbidity (coming from Florida Bay) is the most important factor preventing the establishment of these and other Bahamian species in the Keys. More often, however, the rarity of a species is not so readily explained. A very important thing to realize is that many, if not most, of the small reef species are annuals. Thus, unfavorable environmental conditions during spawning can result in an abrupt and drastic reduction in abundance from one season to the next, as has been demonstrated by Robins (1958) for the gobiid fish *Gobiosoma macrodon* in the Florida Keys. The opposite, of course, can also happen. Short generation time and cyclic fluctuations in size and composition of the gene pool are very important factors in the evolution of coral-reef species.

The tropical western Atlantic fish fauna (as well as that of the tropical eastern Pacific) was derived from the rich Indo-Pacific fauna, elements of which reached the New World at some time prior to the mid-Cenozoic (Rosenblatt, 1963). There are two possible ways in which this could have happened 1) from the west, across the broad, open eastern Pacific; or, 2) from the east, via the prehistoric Tethys Sea. There is considerable evidence, and general agreement among ichthyologists, that the latter route was by far the more important. The Tethys Sea was once located in the area now occupied by the Mediterranean Sea and the countries of the Middle East. As a result, the faunas of the Indo-Pacific had free access to the New World tropics, and many, though by no means all, Indo-Pacific groups succeeded in reaching there. During Miocene times, however, this connection was broken by uplift of the Tethyan syncline, which effectively isolated the Mediterranean and New World faunas from that of the Indo-Pacific. In late Pliocene the final uplift of Middle America occurred, thus splitting the New World tropical fauna in two. Still later, most of the tropical Mediterranean fauna was exterminated as a result of lowered temperatures resulting from Pleistocene glaciation; undoubtedly some of the New World fauna was similarly affected, but to a much lesser degree (Walters and Robins, 1961). As a result of the above series of events, the faunas of the above four areas (eastern Pacific, western Atlantic, Mediterranean, and Indo-Pacific) became progressively less homogeneous with regard to one another, and each proceeded

to develop its own unique characteristics. Because of the extermination of much of its tropical fish fauna and the complete elimination of its living coral reefs, the Mediterranean, despite its intermediate geographical position, has less in common with the other three areas than they do with each other, at least as far as the reef fishes are concerned. For obvious reasons the faunas of the western Atlantic and eastern Pacific are the most similar, with many closely related geminate species, and in some cases the same species, being present in both areas.

The tropical New-World fish fauna is basically a diluted Indo-Pacific fauna. It is characterized by 1) the absence of a number of Indo-Pacific families, 2) nearly always by fewer genera and species than occur in the same families in the Indo-Pacific, and 3) by the near absence of any endemic families (the only exceptions being the Chaenopsidae [Stephens, 1963] and Dactyloscopidae, and some consider the former only to be a subfamily of the Clinidae). However, several distinctive subgroups apparently evolved largely or entirely in the New World, such as the subfamily Gobiesocinae (family Gobiesocidae) (Briggs, 1955), the subtribe Labrisomini (family Clinidae) (Springer, 1959), and the seven-spined species of Gobiidae (Böhlke and Robins, 1968).

The fish fauna of the tropical western Atlantic is substantially richer than that of either the eastern Pacific or eastern Atlantic, particularly with regard to the rock or reef-inhabiting forms. This can be attributed both to the more compressed tropical zones and near-absence of coral reefs in the latter two areas. The fish fauna of the western Atlantic, however, is not nearly so speciose as that of the Indo-Pacific. Starck (1968, pp. 12-13) has estimated that the fish fauna of Alligator Reef, Florida, contains approximately half as many species as areas of comparable size in the Indo-Pacific. Considering that the Indo-Pacific region also is geographically much more extensive than the western Atlantic, it is likely that at least 3.5 times as many kinds of reef fishes (or approximately 2500 species) occur throughout the former area.

Although the Indo-Pacific as a whole is richer than the western Atlantic, this does not tell the complete story. The difference in numbers of genera and species between some groups is much more pronounced than between others, and in one case (the Clinidae) the situation is completely reversed. A comparison of the number

of genera and species of several typical reef families from the western Atlantic and Marshall Islands (Table 1) illustrates these points (data from latter area from Schultz et al, 1953; 1960).

TABLE 1
Comparison of number of genera and species for some marine fish families

	Western Atlantic	Marshall Islands
Acanthuridae	1-4	4-22
Apogoniidae (shallow-water)	3-21	7-32
Blenniidae	6-15	15-35
Clinidae (including Chaenopsinae and Tripterygiinae)	14-60	2-6
Holocentridae	7-11	5-19
Labridae	7-19	21-55
Pomacentridae	5-15	5-41

Although not included in Table 1, the total number of New-World species of Gobiesocidae is approximately the same as for the Indo-Pacific; however, unlike the clinids, this is not true for the genera, which are about three times as numerous in the Indo-Pacific (Briggs, 1955). The large total number of New-World gobiesocid species is, in great degree, due to the explosive evolution of the subfamily Gobiesocinae (particularly the genus *Gobiesox*) in the eastern Pacific.

The most notable exception to the rule of greater species numbers in the Indo-Pacific is seen in the family Clinidae. A partial explanation for this may be that competition from the closely related blenniids has prevented extensive clinid speciation in the Indo-Pacific, whereas many of the ecological niches occupied by the blennies in the Indo-Pacific are taken over by the clinids in the New World (Starck, 1968, p. 13). Another interesting aspect to this is that only about half the approximately 15 western Atlantic blenniid species are characteristic components of the tropical reef fauna (Böhlke, 1959; Springer, 1962, 1967; Randall, 1966), whereas the others occur in rocky situations outside the limits of living coral reefs. Of these, most reef-inhabiting species belong to the subfamily Salariinae, whereas most non-reef forms are of the subfamily Blenniinae (V. G. Springer, *pers. comm.*). In contrast, no western Atlantic clinid species lives totally out of the reef area. This situation differs somewhat from what one finds in the eastern Pacific,

where five genera of clinids (including 13 species) are entirely restricted to cool waters (*Alloclinus, Cryptotrema, Gibbonsia, Heterostichus,* and *Neoclinus*) (Hubbs, 1952, 1953, 1954).

One of the most noticeable differences between the western Atlantic and Indo-Pacific reef faunas is the relative contributions, in terms of biomass, of certain fish families. This cannot be attributed solely to differences in species numbers, although it may be factor. In the western Atlantic the grunts (Pomadasyidae) and sometimes the snappers (Lutjanidae) may occur in tremendous numbers, a phenomenon one does not usually see in the Indo-Pacific (where the Pomadasyidae is largely replaced by the closely related, or identical, Gaterinidae). In the Indo-Pacific the surgeonfishes (Acanthuridae) and cardinalfishes (Apogonidae), in particular, are much more important, in terms of total weight, than in the western Atlantic.

Although we are primarily concerned with the western Atlantic reef fishes, it is necessary to consider briefly those fishes living in other habitats as well. Robins (1971) recognizes two kinds of tropical fish faunas, Continental and Insular. Continental faunas live in regions where environmental change is the rule (temperature, salinity, and turbidity), whereas Insular faunas occur in regions of great environmental stability. Turbid waters, muddy or silty bottom, and absence of coral reefs are characteristic features of the continental habitat, just as clear water, bottom sediments composed mainly of calcium carbonate, and extensive coral reef development are usual features of the insular habitat.

Certain fish families are primarily continental in distribution, although none (at least of those containing more than a few species) is exclusively so. Typical continental families in the western Atlantic include the Sciaenidae (of which all but six of the over 60 western Atlantic species are continental), Batrachoididae (only one of 24 is insular, and that perhaps not entirely so; Walters and Robins, 1961), Sparidae, Ophidiidae, Bothidae, and Cynoglossidae. Some, such as the Gobiidae, are about equally divided with regard to numbers of continental and insular forms, and others (e.g., the Pomadasyidae) contain mostly insular forms. The family Carangidae in general, as well as certain individual species in other families (the sphyraenid *Sphyraena barracuda,* the gobiids *Bathygobius soporator* and *Gobionellus boleosoma,* the gerreids *Eucinostomus ar-*

genteus and *E. gula,* the blenniid *Blennius cristatus,* the ophichthid *Myrophis punctatus,* and the lutjanids *Lutjanus griseus* and *L. jocu*), seem to be at home in either type of environment. All of these are wide-ranging forms that evidently have an unusual ability to adapt to a wide variety of ecological conditions. Those families essentially limited to continental waters would be expected to have limited mobility, both during larval and adult stages. Although some do (e.g., the Batrachoididae), this is by no means always true. As Robins (1971) points out, one of the most characteristic continental species is the Spanish mackerel (*Scomberomorus maculatus*), and only one of the nine Florida species of the ophichthid eel genera *Ophichthus, Bascanichthys, Echiopsis,* and *Letharchus* (a deep-water species of *Ophichthus*) occurs in the Bahamas. All of the above are highly pelagic at some stage of their life history, and there is nothing to prevent them from reaching insular areas. This brings up a most important point, which Starck (1968) and Robins (1971) have clearly shown: that the distinctions between the continental and insular faunas are due in much greater degree to ecological barriers than to physical barriers to movement.

The tropical continental fauna may be divided into northern and southern components (Robins, 1971), the former extending from central Florida (or in summer from the Carolinas) southward toward the tip of Florida and around the Gulf of Mexico to Yucatan; the latter extends from Yucatan southward. Exceptions to this occasionally occur; for example, the northern sciaenids *Menticirrhus littoralis* and *M. americanus* have been collected in the Caribbean (Roy D. Irwin, *pers. comm.*), and the southern sciaenid *Bairdiella sanctaeluciae* has recently been taken on the lower east Florida coast (specimens in Unversity of Florida and Cornell University collections). Of the 30 species of Sciaenidae recorded for Venezuela (Cervigón, 1966, pp. 499-539), however, only six occur in Florida (four in the Bahamas); all but one (the above *B. sanctaeluciae*) are clear-water inhabitants (atypical for sciaenids) of the genera *Equetus, Odontoscion,* and *Umbrina,* and have insular, rather than continental, distributions. Of the 26 species recorded from Guyana by Lowe (McConnell), 1966, only *B. sanctaeluciae* and the insular *Equetus lanceolatus* also occur in Florida. This distribution even holds at the generic level, inasmuch as only seven of the total of 21 sciaenid genera are common to both the Guianas and Florida. As

might be expected, those families of greater mobility are more likely to have species of wide distribution. Thus, of the six species of the eel family Ophichthidae (not including two species of Echelinae) listed by Cervigón (1966, pp. 186-197) from Venezuela, three (*Echiopsis intertincta, Ophichthus gomesi,* and *Ophichthus ocellatus*) are also elements of the Florida continental fauna.

The insular fauna extends, in pure form, from the Bahamas southward through the West Indies. Because of its area and extent of coral-reef development, the Bahamas may be considered to be the center of the western Atlantic insular fauna. Bermuda and the islands of the Fernando Naronha group (off the eastern hump of Brazil) are distant outposts of this fauna. Varying degrees of mixing of the insular and continental faunas occur in Florida, the Greater Antilles, Trinidad, and along much of the Central and South American coasts. The richness of the Florida Keys fish fauna is due in large degree to this mixing effect (Starck, 1968, p. 10).

In contrast to the continental groups, one finds a number of families in which all species (in the western Atlantic at least) are more-or-less strictly confined to an insular habitat. This includes the Chaetodontidae, Holocentridae, Apogonidae, Clinidae, Scaridae, Labridae, and perhaps the Pomacentridae. For the first two families this is invariably true, as it is for the Labridae (if one does not consider the two northern cold-water genera *Tautoga* and *Tautogolabrus*). However, some of the other families contain representatives which, though found in a basically insular environment, seem to require a certain degree of continental influence. For example, the clinid *Starksia ocellata* is always found in rocks or reefs and is one of the most common of the Florida Clinidae. It is absent from the Bahamas, but occurs in the Greater Antilles and along the Central and South American coasts (Gilbert, 1971). Other examples are the apogonid *Astrapogon alutus* and the scarid *Nicholsina usta,* both of which are absent from the Bahamas and present in Florida, where they are especially common along the west coast.

The insular fauna of the western Atlantic, in contrast to the continental fauna, is characterized by relative homogeneity; and some species, nearly all with long-lived pelagic larvae, have very wide distributions. For example, *Labrisomus nuchipinnis* (Clinidae), *Rypticus saponaceus* (Grammistidae), *Holocentrus ascensionis* and *Myripristis jacobus* (Holocentridae), *Bothus lunatus* (Bothidae),

Acanthostracion quadricornis (Ostraciidae), *Pomacentrus leucostictus* and *Chromis insolatus* (Pomacentridae), *Diodon holacanthus* (Diodontidae), *Epinephelus adscensionis* and *Paranthias furcifer* (Serranidae), *Malacanthus plumieri* (Branchiostegidae), *Scorpaena plumieri* (Scorpaenidae), *Mulloidichthys martinicus* (Mullidae), *Acanthurus bahianus* and *A. coeruleus* (Acanthuridae), *Balistes vetula* and *Melichthys niger* (Balistidae) all range from Florida to Ascension Island and/or St. Helena or beyond (Cadenat and Marchal, 1963). The vast majority of insular species, however, have much more restricted distributions. Florida, for example, has eight apparently endemic reef or reef-associated species (*Hypoplectrus gemma* and *Liopropoma eukrines* [Serranidae], *Lythrypnus phorellus, Gobionellus stigmaturus,* and *Ioglossus calliurus* [Gobiidae], *Starksia starcki* [Clinidae], *Emblemariopsis diaphana* [Clinidae, subfamily Chaenopsinae], and *Ophidion selenops* [Ophidiidae]. In addition, the pomacentrid *Chromis scotti,* though recently discovered in the Bahamas (C. R. Robins, *pers. comm.*), probably should be included in this group. Although some of the above will likely be discovered elsewhere, others probably will not. For example, *Hypoplectrus gemma* is a fairly common, readily-observed species in tropical Florida waters, and it seems unlikely that such a distinctive fish would have been overlooked elsewhere. Other western Atlantic reef species undoubtedly have equally restricted distributions, although collections outside of Florida are not yet complete enough to know just which species are involved, particularly the deeper-living forms. The main point, however, is that there is no clearcut division of the insular fauna into northern and southern components, as there is for the continental fauna. Of the 23 species of Clinidae (including the Chaenopsidae and Tripterygiidae) reported by Cervigón (1966, pp. 660-689) from Venezuela, 14 occur in the Bahamas and 13 in Florida. This contrasts sharply with the very dissimilar sciaenid faunas in these two areas (see above).

The only island in the tropical western north Atlantic that is sufficiently isolated that it could be a significant center of endemism is Bermuda. This island, however, possesses relatively few endemics, only 14 forms (or about five per cent) presently falling into this category, none of which is very strongly differentiated (Collette, 1962; Caldwell, 1965; Briggs, 1966). The fauna is, in fact, on the depauperate side, particularly with regard to the small cryptic reef

species. This problem has been discussed by Briggs (1966), who points out that Bermuda is located sufficiently far north as to have been adversely affected by the cooling effects of the various Pleistocene glaciations. Insufficient time has elapsed since the last (Wisconsin) glacial period to permit recruitment and subsequent evolution of a highly endemic fish fauna.

The only other area in the tropical western Atlantic that would be predicted to harbor a substantial endemic fauna is the coast of extreme eastern Brazil, including the offshore islands of the Fernando Naronha group. This area has living coral reefs, and is over 1000 miles from the next closest area of extensive reef development (i.e., Trinidad) (Böhlke and Chaplin, 1968: inside front cover). Not only is the coastline to the northwest largely devoid of favorable habitat for most reef species, but two major river systems (the Amazon and Orinoco) empty large volumes of turbid, hyposaline water into the intervening ocean. One would expect, as a result of this isolation, for some faunal endemism to have developed, and the few available collections from this area indicate that such is indeed the case.

This is not to say that all insular faunas will be as noticeably homogeneous as that of the western Atlantic. For example, in the eastern Pacific the long, linear open shoreline of the western Middle American coast (punctuated by widely separated rocky outcrops); the absence of fringing coral reefs along shore and the near-absence of closely adjacent offshore islands; the presence of distant offshore islands (Galapagos, Cocos, Clipperton, and the Revillagigedos); cold upwellings at various points along the coast; and the geographical and physical nature of the Gulf of California have resulted in numerous pockets of endemism among the basically insular fish groups. In contrast, the tropical western Atlantic is a circular, semi-enclosed sea, containing numerous closely-adjacent islands; and with rich coral growths present around nearly all the islands and bordering much of the shoreline. In addition, the Gulf Stream flows through the Caribbean Sea, Gulf of Mexico, and up the Florida Straits between the Bahamas and Florida. This current is very important in distributing the pelagic larvae or adults of many kinds of organisms, either directly or as a result of subsidiary "spin-off" currents (Caldwell, 1963).

I have reviewed a number of papers on western Atlantic reef

fishes to see if I could find evidence of specific distribution patterns. The results have not been very conclusive. There is some evidence that distinct patterns do exist, although considerably more work is necessary before these can be accurately delineated. To take one example, the gobiid *Gobiosoma louisae* and the holocentrid *Adioryx poco* have been recorded only from the Bahamas, Grand Cayman Island, and Providencia (Old Providence) Island. This may be due in part to the fact that neither of these species lives in very shallow water; however, it could well be significant that neither has been collected in Puerto Rico or the Virgin Islands, despite extensive deep work by Dr. John E. Randall.

Although living coral reefs in Florida are found only a short distance north of Miami, the ranges of a number of reef-inhabiting fish species extend considerably farther northward. Recent exploratory fishing by the U. S. Bureau of Commercial Fisheries has revealed that apparent resident populations of reef species such as *Holocentrus ascensionis* and *Myripristis jacobus* (Holocentridae), *Chaetodon sedentarius* and *Holacanthus tricolor* (Chaetodontidae), *Anisotremus virginicus* (Pomadasyidae), and *Bodianus pulchellus* (Labridae) occur much farther north (to Cape Hatteras, North Carolina) than was previously realized (Anderson and Gutherz, 1965). These fishes live in rocky outcroppings offshore, where they are restricted to somewhat deeper water than is usual for more tropic latitudes. Their restriction to these deeper waters is occasioned by the cold winter temperatures inshore, coupled with the moderating effects of the Gulf Stream offshore. The scarcity of favorable habitat inshore may also be a partial, though less important, factor. A few of the reef species maintain permanent populations in rocky inshore areas along the Florida coast, at least as far north as Matanzas Inlet (ca. 50 miles south of Jacksonville). The most notable of these is *Labrisomus nuchipinnis* (family Clinidae), a hardy, wide-ranging species that occurs south to eastern Brazil and across the Atlantic to West Africa (Springer, 1959, p. 486). This species is excessively abundant in rocky situations along the Florida coast, much more so than it ever is in coral-reef areas, where it must compete with other closely related species. Other reef species found here include *Starksia ocellata* (Clinidae), *Anisotremus surinamensis* (Pomadasyidae), *Scorpaena plumieri* (Scorpaenidae), and *Abudefduf saxatilis* and *A. taurus* (Pomacentridae)

(Gilbert, 1969). The last four species, however, may not represent permanent populations, but instead may be the result of a more or less continuous recruitment of eggs and young from the south, which are carried north and deposited by the Gulf Stream. In addition, this rocky shoreline is also inhabited by certain other species that either are rare in the tropics or do not occur there at all; *Gobiesox strumosus* (Gobiesocidae), and *Hypleurochilus geminatus* and *Hypsoblennius hentzi* Blenniidae). Similar extensions of the tropical reef fauna are known from the eastern and northern Gulf of Mexico (Briggs, 1958; Caldwell, 1959, 1963; Springer and Woodburn, 1960; Caldwell and Briggs, 1957; Briggs and Caldwell, 1957; Dawson, 1962, 1963), as well as for the western Gulf (Hoese, 1959; Springer and Hoese, 1958; Briggs, Hoese, Hadley, and Jones, 1964). They apparently represent a mixture of both resident and non-resident species, the latter of which are annually recruited from the south but do not survive the cold winter temperatures.

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